

Non-nutritional effects of mycorrhizal infection

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INTRODUCTION

The mycorrhizal habit has been described as 'a universal symbiosis' (NICOLSON, 1967) and we recognize that the association occurs in practically every terrestrial ecosystem and in an infinitely large variety of soil conditions. The most commonly observed effect of infection is an enhancement of tissue phosphorus concentration, and yield responses arising from this effect have been widely reported (HARLEY & SMITH, 1983). Even when other physiological responses to infection have been seen they have frequently been considered to be secondary effects of the increased nutrient status. While on many occasions the primary effect is undoubtedly nutritional it is unlikely that throughout the vast range of edaphic circumstances in which the symbiosis prevails its major effect is to provide increases of P inflow to plant roots. The problem is to design experiments which provide adequate discrimination between nutritional and non-nutritional effects so that primary and secondary responses can be identified. In some areas, for example the study of the mycorrhizal role in plant water relations this discrimination is now being achieved. In others, ambiguity remains, and while the responses observed may have a non-nutritional component they cannot be said to be primarily of this nature. Thus, for example, increases of vascularisation which have been observed in plants infected with both VA (DAFT & OKUSANYA, 1973) and ecto-(MASON *et al.*, 1977) mycorrhizas could arise as a result of enhanced nutrient supply, hormonal effects upon differentiation processes, or by a combination of both. While we know that hormones are produced by VA (BAREA & AZCON-AGUILAR, 1982) and ectomycorrhizal (RUDAWSKA, 1982, EK *et al.*, 1983) fungi and that hormonal changes occur in the plant in association with infection (ALLEN, 1980; 1982) there is, as yet, no evidence to show that fungal hormones exert their effects directly by moving into the plant. Further, practically all of the changes of hormone balance seen in the infected plant would be expected to arise if nutritional status or water balance were manipulated independently of infection. ALLEN (1985) describes the many key points at which physiological processes of the plant can be changed both by mycorrhizal infection and by hormone action. We will require a greater knowledge of the mechanisms involved in the integration of these processes before a full understanding of the relative magnitude of nutrient, water and hormonal effects can be obtained. In the

absence of evidence to the contrary, it is safer at present to conclude that hormonal effects associated with mycorrhizal infections are indirect and consequent upon changes of nutrient and water balance.

If we are to progress from the stereotyped view of the mycorrhizal symbiosis to a situation in which we have a broader understanding of its biological role, a profitable approach may be to consider the diversity of situations in which mycorrhizal plants dominate ecosystems. READ (1984) recognized a gradient of environmental circumstances with increasing latitude or altitude along which the predominant type of mycorrhizal infection changed with changing edaphic conditions. There are, of course, changes of nutrient status along the gradient, but of prime importance in determining the changes of vegetation type are non-nutritional factors such as pH and water availability (Fig. 1). While there is a risk of over-simplification, the notion that there has been selection for different mycorrhizal structures in response to changes of pH and water availability provides a useful framework within which to discuss non-nutritional effects of the symbiosis. The presence of an altitudinal gradient of this kind has recently been confirmed in a study of northern temperate forest ecosystems (GIRARD & FORTIN, 1985).

Mycorrhizas and plant water relations. No area of mycorrhizal research has been more neglected than that of host-fungus water relations. This is not because mycorrhizas cease to be important in the arid zones of the world. On the contrary, in this part of the environmental gradient plants with VA mycorrhizas predominate. LINDSEY (1984) concluded from an analysis of the literature that in 89 species of shrub representing 30 families in arid or semi-arid zones throughout the world, 81% had been recorded to be mycorrhizal. By no means all of these regions have phosphorus deficient soils, indeed in some, high levels of infection are found in soils with high concentrations of extractable P. Despite this, until recently few studies of the physiology of host-fungus water relations have been undertaken, and those studies have often involved comparisons between mycorrhizal and non-mycorrhizal plants in which the results are inevitably confounded by enhancement of nutrient uptake in infected plants.

It is the belief of some workers (NELSEN & SAFIR, 1982; GRAHAM & SYVERTSEN, 1984; SAFIR & NELSEN, 1985) that the increases of transpiration or stomatal conductance frequently observed in such experiments following infection, are all secondary effects of enhanced P nutrition. Calculations based upon rates of inflow of P into infected onion plants have led to the view that only trivial quantities of water can be supplied to plants through VA hyphae (COOPER & TINKER, 1981). However, there is a danger in generalizing from observations made under a particular set of experimental conditions and research in more ecologically appropriate circumstances is required before the role of hyphal transport of water can be resolved. Considerable progress in this direction has been made by ALLEN and his group working in the semi-arid short grass prairies of western N. America. The two co-dominant plants of this biome *Bouteloua gracilis* and *Agropyron smithii* show a strong physiological response to mycorrhizal infection. In infected plants photosynthetic rates were increased by 80 and 30% and stomatal resistances decreased by 50 and 30% respectively (ALLEN *et al.* 1981). In subsequent studies ALLEN (1982) showed that large increases of transpiration in *B. gracilis* could be accounted for in terms of water transport through hyphae, though even here the possibility that increases of plant conductance arose through increased P uptake were not excluded. A major advance towards obtaining a distinction between the effects of enhancement of P and of H₂O uptake can be expected

from further studies of *A. smithii* because this plant shows large increases of transpiration, photosynthesis and stomatal conductance following infection with no increases of tissue P concentration (ALLEN, E. 1984). Such responses strongly suggest that hyphal transport of water is directly responsible for enhancement of tissue water balance and this could be an observation of great significance, not only for the ecology and physiology of plants which normally occur in arid or semi-arid, areas but in a wider context because most terrestrial ecosystems suffer periodic droughts which threaten plant survival. A more direct approach to this problem has been adopted by HARDIE (this volume) who has shown that if equilibrium levels of transpiration are measured two days after removing extra-radical hyphae the rates are 6% lower than those before removal. This again suggests a significant direct hyphal contribution to water flux from soil to plant. If this pattern of water transport is seen in VA hyphal systems, there is even more reason to expect it to be important in the more elaborate mycelial structures associated with ectomycorrhizal roots. DUDDRIDGE *et al.* (1980) showed that water could be transferred through ectomycorrhizal mycelial strands and that the strands contain vessel hyphae which present particularly favourable pathways for water transport. When such strands connecting pine seedlings with moist peat were cut, rapid fall of leaf water potential were observed by BROWNLEE *et al.*, (1983) which again suggests that water supply to the shoot has been interrupted. By continuously monitoring the processes of transpiration and photosynthesis before, during, and after cutting of mycelial strands connecting pine and birch seedlings to moist peat, it has been shown that reductions of transpiration in excess of 40%, and of photosynthesis in excess of 25% are obtained in both species (BOYD *et al.*, this volume). Such results confirm that mycorrhizal mycelia form a functional extension of the root system in which the role of water absorption may be of paramount importance. The maintenance of a large external mycelium may therefore be a feature of particular significance in semi-arid areas and it is interesting that ectomycorrhizal fungi such as *Pisolithus tictorius* which are successful in drought stressed habitats, produce particularly prolific mycelial systems (SCHRAMM, 1966), as do VA fungi in these situations (ABBOTT & ROBSON, 1985).

Mycorrhizas and heavy metal resistance. While the production of a prolific external mycelium is advantageous in terms of providing access to growth limiting resources such as water, it could be disadvantageous in situations where the soil solution contains elevated levels of potentially toxic metal elements. Because the solubility of most metals increases with decreasing pH, the natural environments at the acidic end of the gradient are most likely to suffer from metal toxicity (Fig. 1). Ericaceous plants become dominant in the most acidic natural environments and are frequently found also on mine spoils. It has been shown that their characteristic ericoid mycorrhizal infection confers resistance to both copper and zinc toxicity (BRADLEY *et al.*, 1982). The mycorrhizal fungus *Pezizella ericae* has an inherent ability to grow in concentrations of metal which are several orders of magnitude higher than those which the non-mycorrhizal plant can tolerate. More recent studies (HASHEM *et al.*, this volume) show that ectomycorrhizal fungi have lower resistances to copper and aluminium than those found in ericoid fungi. It is evident, however, that within the ectomycorrhizal fungi interspecific differences occur on levels of resistance to both metals. Thus *Suillus bovinus* for example has a lower resistance than *Amanita muscaria*. There may therefore be selection in the natural environment for particular fungi based upon levels of metal resistance. Differences in pattern of accumulation of metals in

sporophores, many of them mycorrhizal, have been observed by TYLER (1980).

In the ericoid fungi there appears to be a generic resistance to metals and little evidence for selection of specially resistant strains could be found in a polluted environment. We are currently investigating races of ectomycorrhizal fungi isolated from sporophores growing on mine spoil. A metal resistant strain of VA endophyte has been described from zinc spoil by GILDON & TINKER (1981), who found that the commonly occurring strains of *Glomus mosseae* were even more sensitive to heavy metals than were the roots of their host plants. Because they occur predominantly in soils of pH above 5.0 (Fig. 1), VA fungi may normally be exposed to relatively low levels of metals which could explain their apparent sensitivity. Their susceptibility to acidic conditions (DANIELS & TRAPPE, 1980) may, indeed, arise through effects of pH upon metal solubility. WANG *et al.*, (1985) propose that aluminium toxicity may be responsible for the inhibition of course endophytes in soils with pH below 5.5, because infection by these fungi is virtually eliminated at Al levels as low as 2 ppm. Even allowing for the fact that the inhibition of infection may be partly a reflection of host sensitivity to the metals it appears that the course VA endophytes are far less tolerant of Al than any of the ecto- or ericoid fungi so far examined. Once again, therefore, the pattern of distribution of mycorrhizal fungi along the environmental gradient appears to reflect response to non-nutritional factors. In this case interactions between pH and metal ions are of crucial importance.

Mycorrhizas and resistance to organic acid toxicity. Along the same gradient of decreasing pH, the turnover of organic matter declines and the concentration of aromatic and aliphatic residues increases in the accumulating parent material. JALAL & READ (1983) identified a wide range of water-soluble phenolic and fatty acids in alkaline extracts of mor-humus soils under *Calluna vulgaris*. Many of the compounds isolated are known to have phyto- or fungitoxic properties. It has since been shown (BAJWA 1985) that when these acids are added to nutrient solutions at concentrations similar to those occurring in soil extracts most of them are toxic to non-mycorrhizal ericaceous plants (Fig. 2). Mycorrhizal infection provides protection against most of the phenolic acids and root growth can actually be stimulated by addition of these compounds relative to that seen in controls. Recent studies by LEAKE in our laboratory demonstrate that at low concentrations most of the phenolic acids can be used as carbon sources by *Pezizella ericae*. The short-chain fatty acids, in contrast, are not used by the fungus and are indeed highly fungi-toxic. This would explain the absence of a beneficial effect from infection (Fig. 2). One of these compounds is known also to be toxic to an ectomycorrhizal fungus (PEDERSEN, 1970; LODE & PEDERSEN, 1970) but there is an urgent need for a wider screening of both the distribution and effects of organic acids in forest soils.

Mycorrhizas and disease resistance This is a neglected area of research. Mycorrhizas might increase disease resistance simply by improving the vigour of the host plant. In addition, by dominating the environment around the root, mycorrhizal fungi may exclude pathogens simply by their physical presence, by the production of antibiotics, or by competition for resources. The sheath and prolific external mycelium of ectomycorrhizal roots would be expected to provide a particularly effective barrier to pathogens, and there is some evidence for a protective role of the symbiont in economically important diseases of both *Pinus* and *Eucalyptus* (MALAJCZUK, 1985). As yet we are not in a position to discriminate between

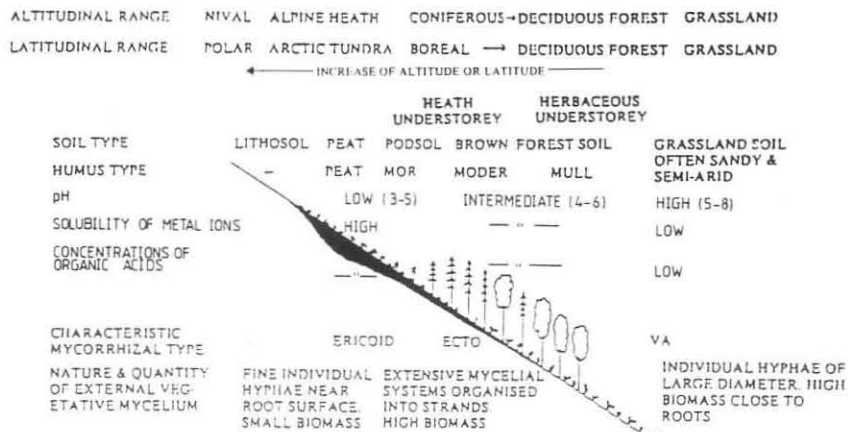


Fig. 1. Diagrammatic presentation of latitudinal and altitudinal gradient of soil conditions and mycorrhizal types.

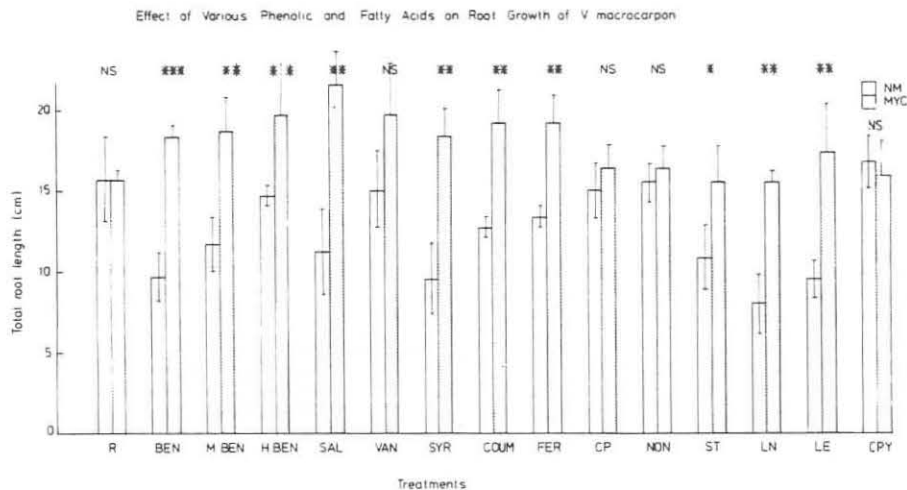


Figure 2. Root lengths of seedlings of *Vaccinium macrocarpon* after growth in the mycorrhizal (MYC) and non-mycorrhizal (NM) condition for 30d in 1/4 strength mineral solution containing different aromatic or aliphatic acids at a concentration of 0.3 mM. (R: control; BEN: benzoic; M-BEN: methoxybenzoic; VAN: vanillic; SYR: syringic; SAL: salicylic; COUM: coumaric; FER: ferulic; CP: capric; NON: nonanoic; ST: stearic; LN: linolenic; LE: linoleic; CPY: caprylic) for 30 days. Values given are means of 4 replicates. Vertical bars represent 95% confidence limits. * indicates difference significant at $P < 0.05$, ** at $P < 0.01$ and *** at $P < 0.001$. NS = Not significant.

direct benefits arising from exclusion of pathogens, and those more indirect effects associated with nutrient enrichment and increase of vigour in the host.

The role of infection in vegetation succession. Disturbance within any of the climax vegetation systems seen along the gradient, whether arising through the activities of man or through natural causes, leads to successional processes in which mycorrhizal infection may play an important role (REEVES *et al.*, 1979, ALLEN & ALLEN, 1980, 1985; JANOS, 1980a b). Primary colonists of disturbed sites are frequently non-mycotrophic 'ruderals' (GRIME 1979), plants in families such as the Chenopodiaceae, and Cruciferae being abundant. In sage-brush communities, a succession has been observed from the non-mycotrophic chenopod *Salsola kali*, through facultatively mycotrophic grasses, to a climax vegetation dominated by obligately mycorrhizal species. Such changes are assumed to arise from increasing competition for nutrients. In most studies which have demonstrated an effect of mycorrhizal infection on the outcome of inter-specific competition, the response has been interpreted in terms of greater efficiency of nutrient capture in the successful species (FITTER, 1977; HALL 1978; JANOS 1980b) so that, in the field, a succession towards obligate mycotrophy would be seen to arise as a result of increasing competition for nutrients as stability returned. However, the situation is undoubtedly more complex than this. Recent studies (ALLEN & ALLEN 1984) have shown that when *S. kali* is grown in competition with two mycotrophic grasses which are characteristic of later stages in the succession, the presence of mycorrhizal fungi leads to decrease of stomatal conductance of the chenopod which suggests interactions between the VA fungi and the non-mycotrophic plant. Further, since one of the grasses, *A. smithii* had also been reported to show increases of stomatal conductance and photosynthesis, but no increases of tissue P concentration, on infection (ALLEN 1984), there is good reason to believe that some, at least, of the mycorrhizal effect on successional processes has a non-nutritional basis.

The full scope of possible mycorrhizal effects is yet to be revealed and it is encouraging that ecologists are beginning to recognize their importance in natural ecosystems. The first hundred years of mycorrhizal research has taught us much about the basic physiology of the symbiosis. The next century will lead to refinements of understanding. We shall move on to ask questions about the role of the symbiosis in particular habitats. As we do so, it is almost certain that in addition to learning more of the nutritional benefits, we shall increase our knowledge of the non-nutritional effects, and of the interactions between these two types of response to mycorrhizal infection.

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